MARITIME STRESS TOLERANCE STUDIES OF CALIFORNIA DUNE PERENNIALS

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ABSTRACT

Experimental evidence indicates that *Camissonia cheiranthifolia* ssp. *suffruticosa,* a coastal dune perennial, is excluded from the strandline community due to intolerance of seawater inundation and sand burial. The strandline dune species *Abronia maritima* and *Ambrosia chamissonis* were tolerant of all maritime stresses tested.

RESUMEN

Evidencia experimental indica que *Camissonia cheiranthifolia* ssp. *suffruticosa,* una especie terrenal de médano costero, está escluído de la comunidad de encalle dado su intolerancia de inundación de agua salada y entierro arenal. Las especies de encalle en médanos costeros *Abronia maritima* y *Ambrosia chamissonis* toleraron todas las pruebas de tensión marítima echas [en ellas].

The goal of this study was to identify environmental stresses that are responsible for the observed zonation patterns of three dune species (*Abronia maritima, Ambrosia chamissonis,* and *Camissonia cheiranthifolia* ssp. *suffruticosa*) in coastal San Diego County. In the current (although disturbed) zonation pattern, *Abronia maritima, Ambrosia chamissonis,* and *Carpobrotus* spp. dominate the foredune environment (under occasional tidal influence); *Camissonia cheiranthifolia* ssp. *suffruticosa, Abronia umbellata,* and *Lotus nuttalianus* grow in the backdunes (not typically washed over); and a coastal scrub community composed of *Lotus scoparius, Eriogonum fasciculatum,* and *Encelia californica* occurs further inland.

Environmental stress (defined as any condition reducing plant growth) is not uniform among coastal dune habitats. Many factors vary with proximity to the ocean, so that plants at the driftline routinely encounter greater stress than those inland (Avis and Lubke 1985; Barbour 1978; Lee and Ignaciuk 1985; Oosting and Billings 1942). Species are distributed in rough bands parallel to the coast (Doing 1985; Donnelly and Pammenter 1983; Nakanishi and Fukumoto 1987; and Orme 1973); the zonation is most easily explained by different tolerance limits to these maritime stresses. This species zonation is not stable, however. Distribution limits may expand during benign conditions, but be curtailed by a storm or other disruption. Thus, the distributional patterns of coastal plants may relate

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more to the length of time since the last disturbance than to average conditions at a particular location.

Environmental factors not only vary inland from the beach, but along the coastline as well. Quantities and types of maritime stresses received are unique for each beach depending on such factors as microtopography (Barbour 1978), directional exposure (Travis 1977), recreational use (if any), sand supply, etc. In San Diego County, for example, south-facing beaches may be sheltered from winter storms that approach from the northwest, resulting in less storm-generated disturbance. In addition, coastal canyons funnel episodic Santa Ana winds, causing certain beaches to experience more sand movement than others. Generally, due to low average wind velocities at this latitude (Calif. Dept. Water Resources 1985), wind-mediated stresses (seaspray deposition, sand movement, and sandblasting) are probably not as important as storm-generated ones (erosion, seawater inundation, and sand dumping).

The literature suggests that salt toxicity is limiting to coastal plants (Donnelly and Pammenter 1983; Oosting and Billings 1942; Barbour and DeJong 1977; Boyce 1954; and Malloch 1972). This may result from two processes: seawater enters plants that have been severed by crashing waves and moving sand; seaspray enters the plant after epidermal cells have been sandblasted.

This study evaluated the effects of three stresses (seawater inundation, sand burial, and seaspray) that may limit coastal dune plant growth and survivorship at this latitude. Sea spray deposition was monitored in the field and an overwash experiment took place on a restored dune. Sand burial and nutrient effects were evaluated experimentally at the Pacific Estuarine Research Laboratory (PERL).

Three species of native dune perennials were examined experimentally. *Abronia maritima* (red sand verbena) is a succulent prostrate forb with a long taproot. *Ambrosia chamissonis* (beach bur), another long-lived deep-rooted perennial that is more common than *Abronia* on local beaches, has been characterized as an aggressive foredune builder (Purer 1936; Cooper 1967). *Camissonia cheiranthifolia* ssp. *suffruticosa* (beach evening primrose), a shorter-lived, upright woody perennial, occurs as a pioneer species predominantly on backdunes (Purer 1936). All 3 species have long taproots that quickly penetrate the surface substrate to reach permanently moist sand (up to 2–3 m as investigated at the Silver Strand State Park beach).

Methods

This study was done in southern San Diego County, California (32°30′N, 117°09′W): field work at the Tijuana Estuary/Border Field State Park and the Silver Strand State Park, and experimental work at PERL. Border Field State Park is located on the coast, immediately north of the U.S.–Mexican border. PERL is located east of Border Field State Park, 1 km inland of the Tijuana Estuary river mouth and within the Tijuana River National Estuarine Research Reserve. The Tijuana Estuary barrier beach is highly dynamic due to the presence of the estuary mouth and an artificially narrow beach. Dune wash-over events frequently move sediments into estuary channels, cutting off tidal flow. Management agencies have repeatedly dredged sediments from these channels to maintain the tidal prism necessary to keep the estuary mouth open; these spoils were placed on the upper beach. Vegetation is sparse due to human trampling and wash-over events. The Silver Strand State Park beach is more stabilized and characterized by larger dunes vegetated with *Carpobrotus* spp.

Seaspray deposition was monitored at Border Field State Park. Experimental plantings on the Tijuana Estuary barrier dune were washed over many times during the winter months, providing useful data on the effects of seawater inundation. The nutrient and burial experiments, carried out at PERL, sought specific responses to individual stresses (sand burial and varying levels of nutrients including seawater).

Monitoring of seaspray. Seaspray was collected on 9 filter paper traps (Whatman paper, round with 12.5 cm diameter) as used by Barbour and DeJong (1977), placed vertically 0.3 m above the sand substrate in areas void of vegetation. Traps were left in the field for up to one week at a time, except when a severe wind event occurred when traps were left out for 24 hours. Filters were collected and soaked in 20 ml of distilled water for 5 minutes, and conductivity of the water was measured with a Labline mho meter.

"Natural" wash-over experiment. An experiment was conducted on the restored dune north of the Tijuana River mouth. This dune was inadvertently constructed too close to the surf but proved ideal for quantifying the effects on dune vegetation caused by wash-over events (seawater inundation and storm induced sand erosion/accretion). Due to the intensity of the storm surge and the large amount of sand displaced, the amount of water and sand that the system received was not quantified. However, dune elevations were taken monthly (Fink 1987).

To protect experimental plants from heavy recreational use, three replicate 10 × 10-m areas were enclosed with hogwire fencing. The 10-cm openings between wires did not impede sand flow. Thirty-six (1-month-old) seedlings were planted on 14 June 1986 within each enclosure: 12 each of *Ambrosia chamissonis, Abronia maritima,* and *Camissonia cheiranthifolia.* Plantings were approximately 40 m inland from 0.0 mean lower low water (MLLW). All seedlings were drip irrigated for 2 weeks to facilitate establishment. Following this period, plants received approximately 8 liters of water/week only when dry conditions prevailed. During the first month, plants lost to mortality were replanted. Monitoring of the planted vegetation began 7 July 1986 and ended 15 March 1987. Survivorship and canopy volume were quantified monthly or after a wash-over event. The site was visited at least twice per week.

Sand burial experiment. Dune vegetation may be buried by either wash-over or wind-mediated deposits of sand. A single wash-over event can dump large amounts of sand (up to 2 m) on the vegetation and bury entire plants. The maximum amount of sand deposition is dictated by storm intensity. In contrast, wind blown sand grains are physically impeded during "sand accretion." Here, sand accumulation is related to the height of plants. When all vegetative portions are covered, sand grains are no longer physically impeded. For this reason, wind-mediated sand accretion may result in much less sand deposition at low-wind latitudes such as San Diego County, compared to the "sand dumping" process. In addition, sand accretion does not involve physical contact with the surf.

The sand dumping and sand accretion processes differ in the rate of sand deposition and have different effects on the vegetation. An experiment was designed to compare tolerances of the three species under study to high (as in sand dumping) and low (more similar to sand accretion) deposition rates. The experiment was conducted outdoors at PERL. A 2.5-m deep trench was excavated down to a substrate of coarse grain river sand, then filled with 2 meters of native dune sand taken from the Silver Strand State Park beach. Nine equal 1 × 1-m plots were then created within this trench with plastic sheet dividers secured with wooden stakes. These plastic "walls" prevented contamination of adjacent plots from sand addition treatments. Although no experimental plants were shaded, the plastic may have resulted in higher air and soil temperatures due to heat absorption and reduced wind flow; this was not quantified.

Each plot was planted on 10 April 1986 with three plants of all three species (nine plants), which were randomly assigned. Plants were six months old at planting time and were not fertilized for the duration of the experiment. The soil substrate contained very little organic matter, with the exception of some partially decomposed *Carpobrotus* spp. stems. Plants were watered (soaked) with tap water weekly for the first 6 weeks, then monthly.

Treatment levels of 0 cm, 5 cm and 10 cm of sand addition per month were assigned randomly to the nine plots. These treatments were based on observations of accretion/erosion rates following wind events at local beaches over the previous three years. Three burial treatments were administered starting on 19 May 1986 and ending

4 August 1986. Sand for this purpose was obtained the day of treatment application from the restored dunes at the Tijuana Estuary. Survivorship was quantified on 10 March 1987 by excavating all plants.

Seawater and nutrient experiment. The purpose of this experiment was to test for a response (positive or negative) to seawater and inorganic fertilizer. It is quite possible that small quantities of seawater are beneficial to coastal plants whereas larger quantities limit growth, thus contributing to the zonation pattern. The effects of seawater were tested both as spray on leaves (simulating seaspray) and as liquid on roots (simulating wash-over).

Plants for this experiment were germinated in beds. When they reached the "third-leaf stage" they were transplanted (on 10 June 1986) to standard 1-gallon (3.8 liter) pots (one plant per pot) with native dune sand from the Silver Strand State Park and grown outdoors at PERL. All experimental plants were protected from receiving additional seaspray from the ocean by placing them on the lee side of a trailer.

The following four treatments were administered to three species with four-fold replication of pots on 10 July 1986, and every two weeks thereafter for 16 weeks:

1) Fertilized with 80 g Osmocote brand slow-release fertilizer per pot;
2) Watered with 30 ml of locally collected seawater to simulate seawater inundation;
3) Leaves sprayed with 2 ml locally collected seawater applied to the foliage via an atomizer to simulate seaspray deposition;
4) Control; no nutrients.

Treatment #1 was administered only once at the beginning of the experiment to the surface soil; treatments #2 and #3 were repeated every 2 weeks. In the seawater treatment, seawater was added directly to each pot. Prior to the spray treatment application, the soil surface was covered with a paper towel to prevent any spray from entering the soil. Two ml of seawater was chosen for spraying to mimic natural amounts accumulated on the beach. To determine if this quantity was realistic, plants with filter paper traps situated within the canopy were sprayed with varying amounts of seawater. Traps receiving the 2 ml treatment captured 1600 micromhos/cm of salt. Since this treatment was to be administered every 2 weeks, the daily average was 114 micromhos/cm/day. This quantity was found to be at the lower end of the range of salts collected on filter paper traps observed in the field.

After each treatment application, all control, fertilized, and seasprayed plants were watered with 30 ml of tapwater to compensate

TABLE 1. SEASPRAY QUANTIFICATION. Relative amounts of seaspray deposited per 24 hour period on filter paper traps in 3 dune microhabitats (windward, ridge, and lee) on 5 sampling dates; values are in micromhos/cm.

		Sampling date					
		19 Mar 86	14 Apr 86	9 May 86	17 Jan 87	2 Mar 87	Mean
Windward	mean	1068	1183	1231	1448	2240	1459
	n	2	3	2	3	3	
	SE	41	231	396	54	762	187
Ridge	mean	331	518	808	2250	1833	1297
	n	2	2	2	3	3	
	SE	51	100	39	76	36	337
Leeward	mean	170	187	110	413	1143	467
	n	2	2	2	3	3	
	SE	99	55	10	38	422	153

for the water added to the seawater addition treatment. Plants were rotated prior to treatment application. After 8 treatment applications (16 weeks), the pots were emptied, the stems cut from the roots, and both plant portions washed and bagged separately. These samples were oven-dried at 50°C for 36 hours and weighed.

Seawatered plants were flushed with 50 ml of tap water every 4 weeks to prevent a salt crust from forming on the soil surface (high soil salinities are not normally encountered in the dune substrate). Observations of dune soils at the Silver Strand State Beach before and after precipitation events indicate that 1.5–2.0 inches of rain are required to reach depths greater than 0.5 m. Under average precipitation conditions in San Diego County, 3–4 winter storms produce precipitation with potential for flushing the soil horizon. This would average out to 1 storm/month during the rainy season; thus monthly flushing was chosen for the experimental pots.

RESULTS

Tolerance to seawater as seaspray. Monitoring of seaspray deposition revealed that the protected lee slopes of coastal dunes experience lesser quantities of this stress than the windward or ridge slopes (Table 1). This is consistent with the findings of Barbour (1978) who quantified seaspray deposition in northern California. However, due to much higher daily wind velocities in northern California (Fig. 1), one would anticipate lower seaspray deposition rates in southern California.

The seaspray treatments used in the nutrient experiment were sufficient to scorch *Camissonia* and *Ambrosia*; there was no difference in biomass between seasprayed plants and the controls. Al-

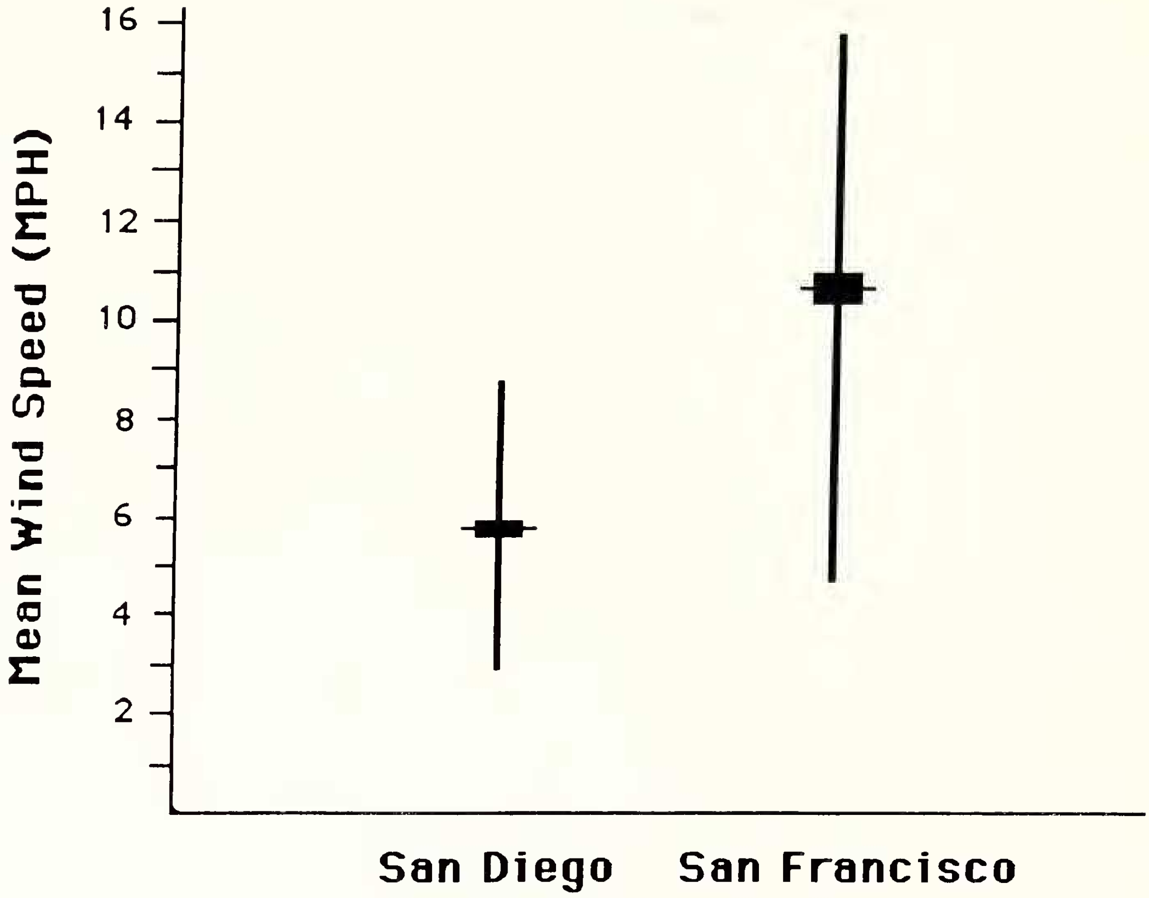

FIG. 1. Contrasting wind speeds (1960–1978) for San Diego (32°42′N) and San Francisco (37°37′N) computed from mean monthly wind values. n = 12 months × 19 years = 228. Horizontal lines are means, rectangles represent ±1 SE; vertical lines are extreme mean monthly values recorded over the 19-year study period. Data from Calif. Dept. Water Resources (1985).

though *Camissonia* leaves were scorched, plants produced significantly more flowers under this treatment (Kruskal-Wallis test, $p < 0.05$; Fig. 2); there was no significant effect on flowering or survival of *Ambrosia* or *Abronia.*

Tolerance to seawater in a wash-over event. Most of the restored dune was washed over many times during the course of this "natural" field experiment. The first wash-over event occurred during the storm of 4 December 1986 (Fig. 3). Although it is uncertain how many times the barrier dune was washed over during this storm season, all 3 plots were inundated at least once, and plots 1 and 2 at least three times. Plants in plot 2 experienced the harshest contact with the surf; here twenty cm of sand was eroded and entire plants were swept away.

Seedlings were probably well established before the storm, based on observations at the adjacent Silver Strand State Park, where excavated seedlings had reached permanently moist sand (1–2.8 m from the surface) within 6 months. Seven (of twelve total) *Ambrosia* plants in plot 2 were washed away, whereas all twelve *Ambrosia*

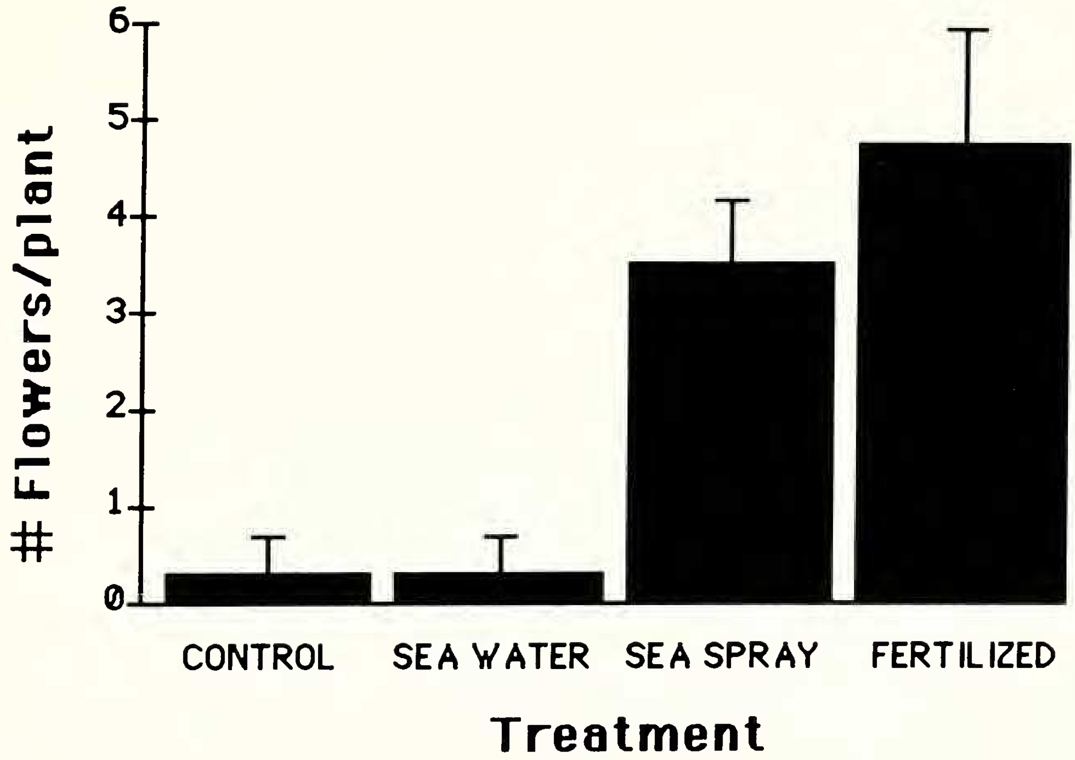

FIG. 2. Numbers of flowers/plant produced by *Camissonia cheiranthifolia* ssp. *suffruticosa,* for each treatment administered in the fertilizer experiment. Error bars are ±1 SE; n = 4.

plants persisted in both plots 1 and 3. Due to these between-plot differences in storm effects, there was high variability in the survivorship curves for February and March (Fig. 3). *Abronia* survivorship decreased steadily from the planting date but did not coincide with storm wash-overs. Mortality likely resulted from overwatering; *Abronia* grew best when planted >1 m from a drip emitter.

There was a second wash-over event on 17 January 1988 (cf. *Shore & Beach* 57[4], special storm issue) that severely eroded the barrier dune at the Tijuana Estuary. Observations following this extreme storm (Fink 1989) showed that *Abronia* has the ability to withstand seawater inundation: *Ambrosia* and *Abronia* resprouted 1 week following this event and resumed growth thereafter. All *Camissonia* were killed; mature plants remained brown and did not resprout. All *Camissonia* seedlings were also destroyed and no new ones appeared in spring 1988.

Results from both "natural" experiments indicate that *Camissonia* cannot withstand repeated seawater inundation. This may explain why it is unable to grow in the strandline environment, where wash-over events are common. However, *Camissonia* growing in the third plot, which was washed over only once, did not perish, indicating that this species can tolerate other maritime stresses such as sand erosion and seaspray deposition (as well as limited quantities of seawater inundation).

Further evidence of *Camissonia*'s inability to tolerate wash-over

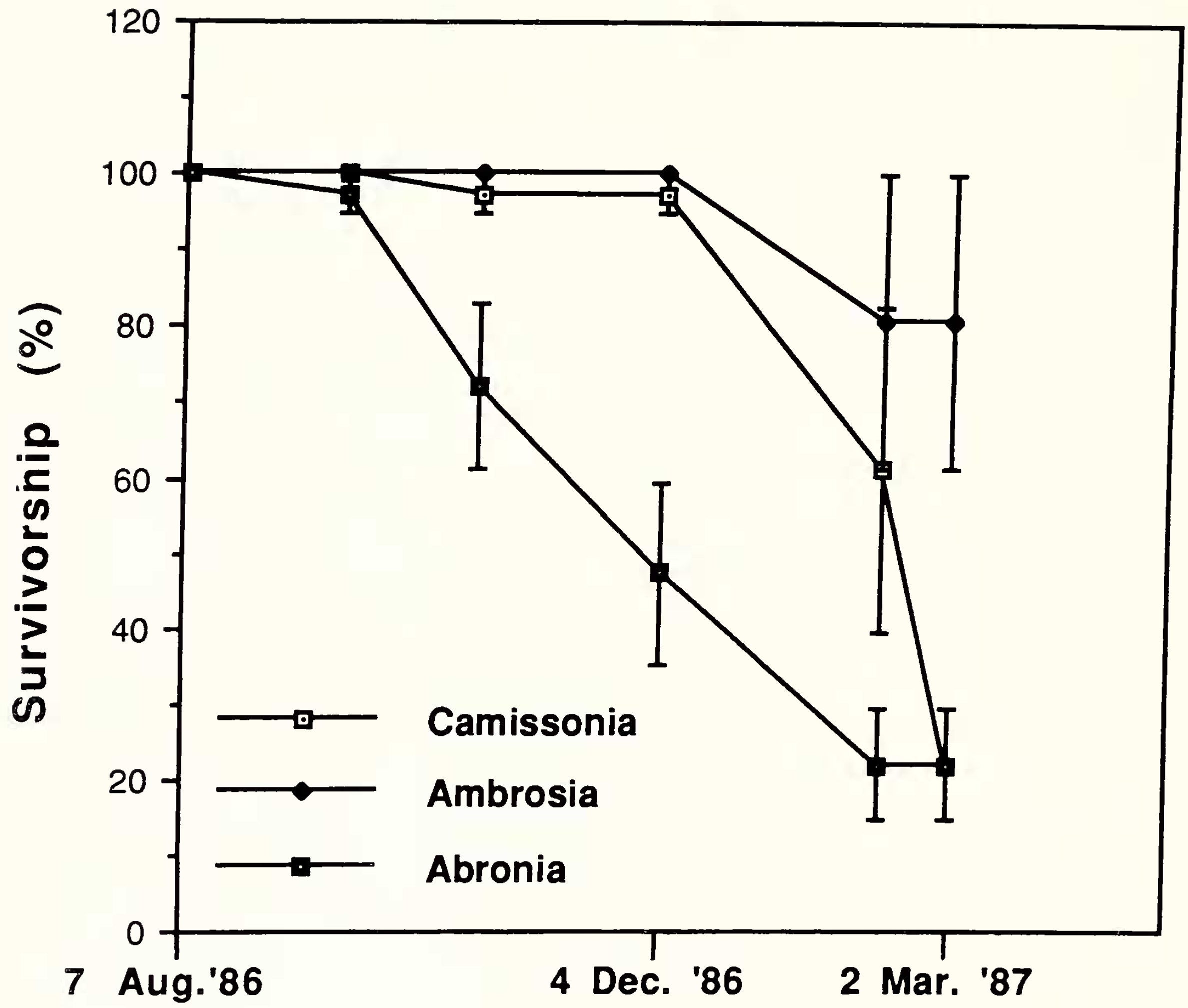

FIG. 3. Survivorship of three species of dune perennials over a 245-day period on the restored dune at the Tijuana Estuary. Note that *Camissonia* and *Ambrosia* mortality coincided with the advent of winter wash-over events (4 Dec 86). n = 34 *Camissonia*, 18 *Abronia*, and 36 *Ambrosia* for all 3 plots combined.

events comes from the nutrient experiment (Fig. 4). Roots of *Camissonia* subjected to seawater inundation were significantly smaller than those of the control plants (one-way ANOVA, $p < 0.05$). Treatments were not significantly different from controls for *Abronia* and *Ambrosia,* with the exception of the fertilizer treatment which increased biomass for both species.

Evaluation of the water table below *Camissonia* growing in a dune slack at the Silver Strand State Park beach indicates that *Camissonia* roots may tolerate exposure to brackish water (less than 5 ppt; Fig. 5). Here the depth to water table fluctuated from 0.97 m in winter to 1.38 m during the summer months (Fink 1987). Roots were excavated at 1.2 m in summer, 1986, indicating that this species may tolerate some exposure to brackish water during the winter months.

Tolerance to sand burial. The three species of dune plants used for this experiment all had different responses to the sand burial treatments (Fig. 6). *Ambrosia* was the most tolerant, and *Camissonia*

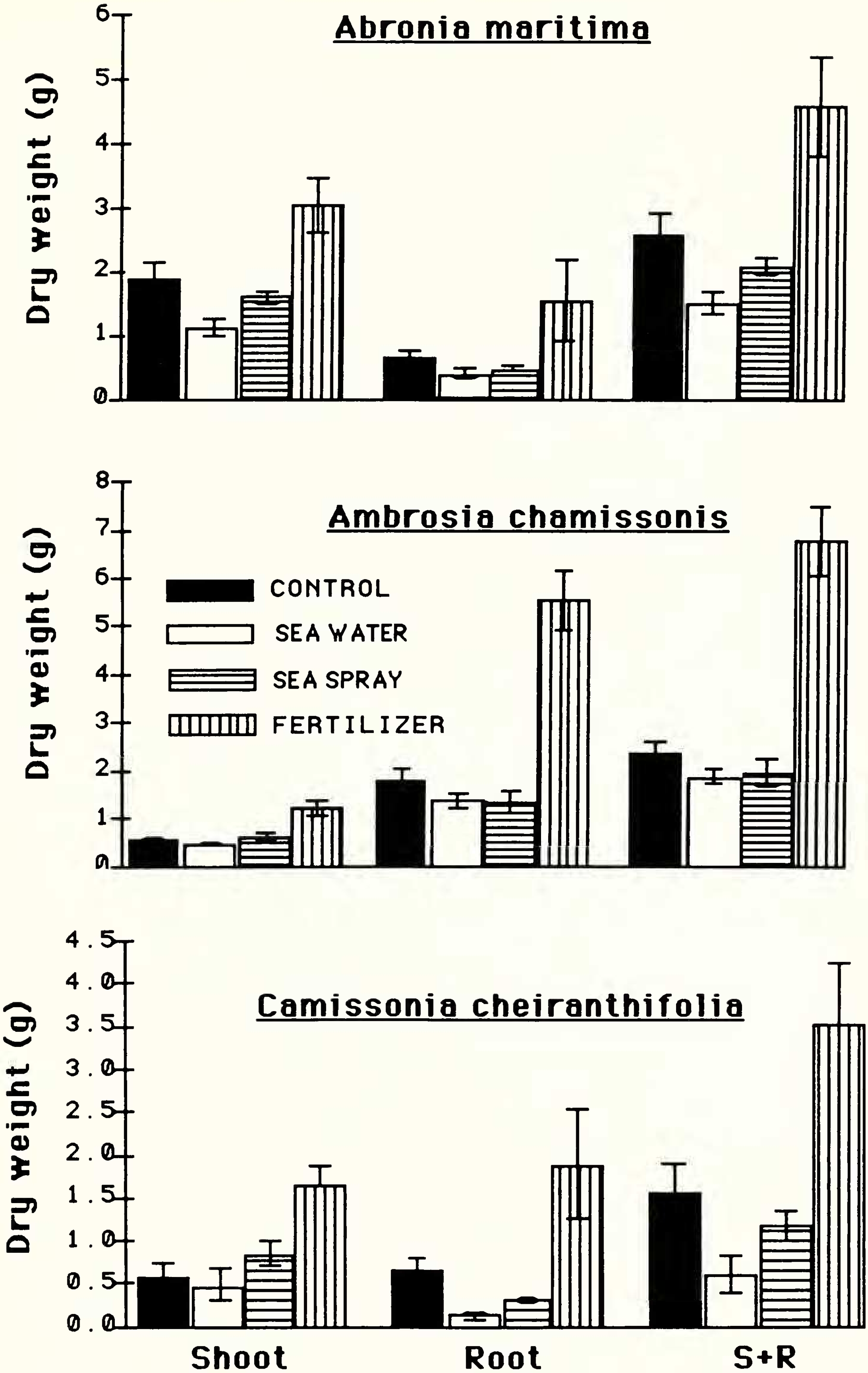

FIG. 4. Response of three species of dune plants to 4 nutrient treatments. Roots of *Camissonia* plants receiving the seawater treatment weighed significantly less than controls. Error bars are ±1 SE; n = 4.

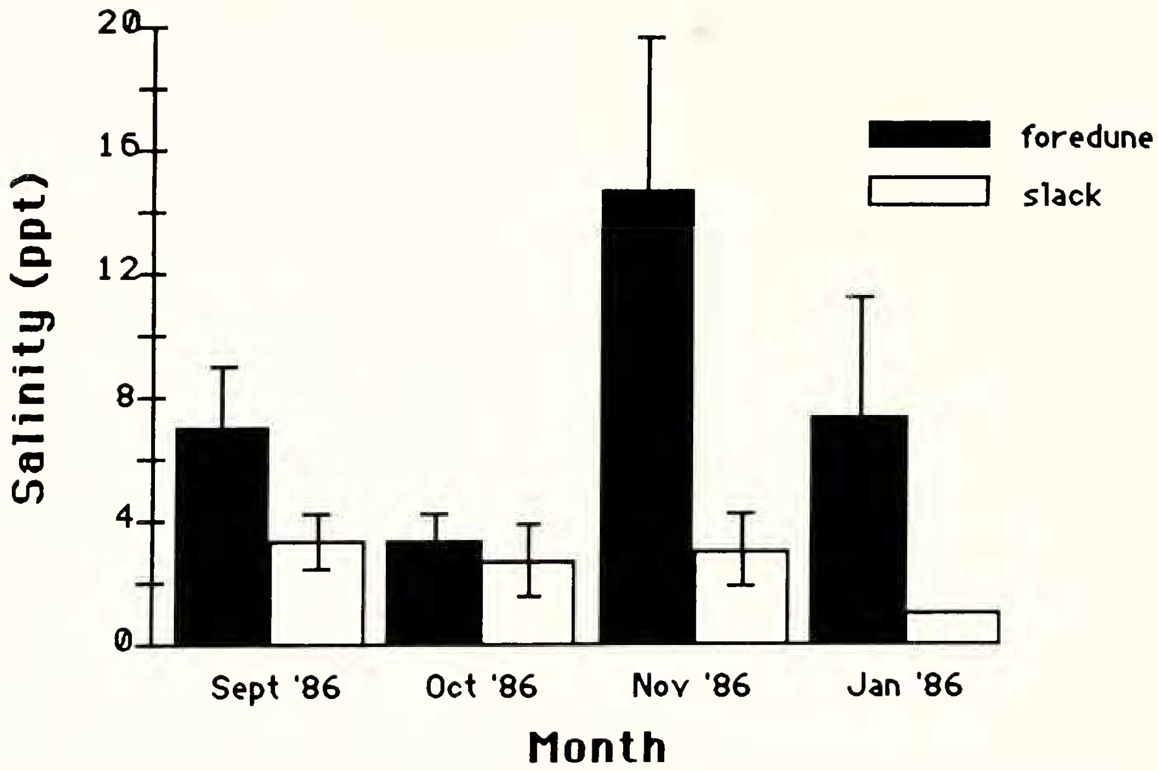

FIG. 5. Salinities in parts per thousand in water table samples taken from foredune and slack sampling sites at the Silver Strand State Park beach. Salinities were taken with a refractometer; samples were taken at 3 m depth for the foredune and 1 m in the slack zones. Error bars are ±1 SE; n = 3.

the least. Inspection of the growth responses throughout the experiment revealed that *Ambrosia* could sprout up through a complete covering of sand; it survived the heaviest burial treatment (10 cm/month; 30 cm total). *Abronia* growth continued only while the apical meristem was not completely covered. Specimens of *Camissonia* died when the central rosette was covered (and remained so) by approximately 20 cm of sand, although the flowering shoots remained above ground. This indicates that *Abronia* and *Camissonia* are tolerant of sand accretion (wind-mediated), but cannot survive "sand dump" (storm-induced). These findings are also supported by Cunniff (1984), who studied the foredune vegetation at Point Mugu (Ventura County, California) before and after the intense storm of February 1983. At Point Mugu, *Ambrosia* emerged through a 1 m layer of wash-over sand, whereas *Camissonia* perished.

DISCUSSION

This study indicates that, in southern California, a distinct zone of beach vegetation is maintained by storm wash-over events. Wind-mediated stresses probably did not limit growth or survivorship of the three species studied in 1986 (or 3 years thereafter). Within the zone of inundation, typically only 4 or 5 strandline species are present following wash-over. These plants could be thought of as "sea-

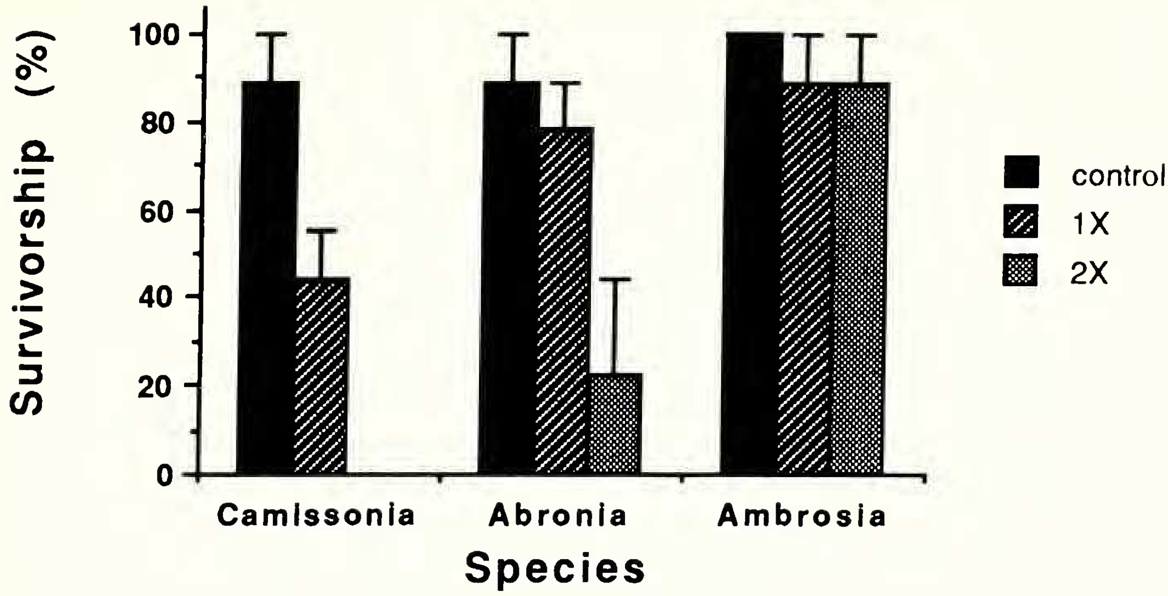

FIG. 6. Percent survivorship for 3 species of dune perennials (six months of age) grown under 3 sand addition treatments: control = no sand addition, 1× = 5 cm/month, for a total of 15 cm after three treatments; 2× = 10 cm/month, for a total of 30 cm after three treatments. Error bars are ±1 SE; n = 9 plants. Percent survivorship for *Camissonia* subjected to the 2× treatment was zero (no bar shown on this graph).

sonal halophytes" due to their ability to deal with inundation for a portion of the year. Others dune species, such as *Camissonia cheiranthifolia* ssp. *suffruticosa* are removed during this dynamic process.

Further inland, out of reach of the storm waves, dune plant species may be salt stressed, but from seaspray. Although the quantity of salts may be substantially less than at the strandline, the chemical composition is potentially more damaging due to ion separation when blown inland (Clayton 1972). In addition, seaspray deposition is chronic in nature, occurring over the entire season. Plants tolerant of chronic seaspray have been termed "aerohalophytes" (Rozema et al. 1982). Microsites within the inland zone may provide some protection from seaspray, allowing intolerant species to occur.

Further experimentation would be appropriate to determine if a "zone of aerohalophytes" is maintained by the effects of seaspray, eliminating plant species more typically found inland (dune scrub, coastal sage scrub, and weedy glycophyte species). Preliminary evidence suggests that this is the case, as mortality of species such as *Lotus scoparius, Eriogonum fasciculatum,* and *Melilotus indicus* has been observed after intense wind events (20 knot winds for at least 4 hours). This zone may be less distinct in San Diego County compared with latitudes where daily wind events cause significantly more salt stress.

Examination of wind patterns (Calif. Dept. Water Resources 1985; Goodridge et al. 1979) suggests that coastal southern California is relatively calm and that strong winds occur only rarely during winter storms and Santa Ana (dry, offshore) wind events. Even during these times, seaspray deposition is minimal. Winter storms are usually accompanied by precipitation, which reduces salt accumulation, whereas Santa Ana winds prevail from the E-NE and are not likely to contain seasalt. Cooper (1967) stated that south of Point Conception (200 km north of San Diego County) the wind "both in velocity and prevailing direction, is relatively inefficient in moving sand from the beach inland." The coast of northern California experiences much higher daily wind velocities; wind mediated stresses would more likely limit dune plants at this latitude.

Seaspray deposition was not sufficient to cause plant mortality during this study. With the low wind velocities that are characteristic of this latitude, seasalts may actually enhance growth (or at least fecundity) of certain dune species. Increased flowering was observed for *Camissonia* when it was experimentally sprayed with seawater.

Other researchers have documented salt-stimulated growth of coastal plants (Lee and Ignaciuk 1985; Okusanya 1979; Rozema et al. 1983), although from seawater inundation rather than seaspray. The water table sampled at the Silver Strand State Park was brackish; perhaps mature plants obtain nutrients from seawater moving laterally below ground.

This study suggests that storm-generated stresses are more limiting than wind-generated ones for the three species of plants tested, using well-established seedlings. However, the reverse might be true for newly germinated seedings. Seedling establishment is perhaps the most vulnerable stage of the life cycle of the dune perennials under study. DeJong (1979) has stated that *Abronia* and *Ambrosia* can become established in southern California only in years with late spring and early summer precipitation events. Once germination occurs following winter rains, seedling roots must grow at a pace that keeps up with a layer of moist sand that recedes as the surface layers dry out. Dune soils sampled at the Silver Strand State Park dropped to near 1% water (by weight) during the summer months in the upper 0.5 m (Fink 1987).

Sand movement can also be problematic for seedlings; they may be eroded away in exposed areas or buried in the dune swales or the lee of hummocks. Dead seedlings of *Cakile maritima* (third leaf stage) were observed after 10 cm of sand was eroded by a Santa Ana wind event. Thus at this latitude, wind generated stresses may be more limiting to growth and survival of seedlings than to mature plants. Additional studies of newly germinated seedlings are needed to improve our understanding of distribution patterns.

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